

Age, Dominance Rank, Natal Status, and Tenure Among Male Macaques

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ABSTRACT Age and rank are often related among males in multi-male groups of macaques. However, recent studies have not consistently reported that age and rank are correlated. This paper reviews studies providing data on at least age and rank for each individual in the sample to investigate how the demographic composition of data samples can affect whether statistical analysis finds significant correlations between age and rank. I reanalyzed data on the age composition, natal status, and length of tenure of the males comprising the samples. Significant nonlinear age-rank relations existed in four of seven studies reviewed. Samples lost statistical significance after removing younger individuals, but at different lower age limits. Samples showing no significant age-rank correlation consisted mostly of adults or natal males. The length of tenure in a troop and natal status showed strong correlations with residuals of the nonlinear age-rank regressions, implying that these factors tend to weaken age-rank correlations, but tenure may have little effect independent of age among males staying in troops longer than about 1 year. The data suggest that the demographic composition of study samples, especially age, may still explain some differences in conclusions among studies on rank and reproductive success focused on “adult” samples. Relatively younger or older males may have contributed to significant correlations between rank and measures of mating success, as they do for age and rank. Primatologists may need to apply nonlinear statistical techniques to samples composed of wide age ranges without subdivision to investigate the causes of both the cross-age and within-age variation in dominance rank or reproductive success. *Am J Phys Anthropol* 105:511–521, 1998.

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Primatologists have used various analytical strategies to account for the effects of age on rank in statistical analyses testing whether rank affects reproductive success. Many studies deliberately limited the study sample to adults to avoid the strong effect of low ranking, subadult males in producing significant correlations between rank and reproductive success. Under these conditions, some studies reported a lack of correlation between dominance rank and measures of mating success (Dewsbury, 1982; Takahata, 1982; Bercovitch, 1986; McMillan,

1989; Paul, 1989; Paul and Kuester, 1996), while other studies disputed those results (Cowlshaw and Dunbar, 1991; Bulger, 1994). In other approaches, researchers analyzed reproductive success in relation to a partial correlation controlling for age (van Noordwijk and van Schaik, 1988), or rank variation within cohorts (Smith, 1994). These

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studies exemplify the importance of ascertaining whether an age-rank correlation exists in multi-male social groups of primates. The cited studies had either shown or assumed that age, rank, and reproductive success are mutually correlated, or that these relations are curvilinear.

However, whether or not age is a major correlate of dominance rank among male macaques (genus *Macaca*) remains in dispute. Many studies have reported that rank is correlated with age among male macaques living in multi-male troops (Norikoshi and Koyama, 1975; van Noordwijk and van Schaik, 1985, 1988; Paul, 1989; Sprague, 1992). Other studies have reported that no age-rank correlation existed in their study groups (Hill, 1987; van Noordwijk and van Schaik, 1988), or that no correlation exists among adults (McMillan, 1989).

Several reasons may exist for the disparity in results. First, the age composition of the study samples may have affected the results of linear or monotonic statistical analysis. Many researchers have postulated that the shape of the age-rank relation may describe an inverted-U because dominance rank among male primates often starts low for young individuals, rises until it reaches a maximum during prime adulthood, and then drops with increasing age (e.g. Cowlshaw and Dunbar, 1991; Dunbar, 1988; van Noordwijk and van Schaik, 1985, 1988; Sprague, 1992). If the age-rank relation is an inverted-U, a linear regression may yield a positive correlation for a sample with many young individuals, a negative correlation for a sample with many old individuals, and no correlation for a narrow sample composed of only adults, or a broad sample encompassing young to old individuals. Nonlinear regressions may be preferred, especially if further analysis uses the residuals of the regression.

Second, many variables, most importantly natal status and tenure, may weaken a potential age-rank correlation. Drickamer and Vessey (1973) reported that tenure in a troop explained more of the variation in male rank than age. Hill (1987) reported that rank was correlated with tenure but not age. Natal males often hold high rank, and rank among natal males is often determined

by maternal rank rather than age (Chapais, 1983; Drickamer and Vessey, 1973; Koford, 1963; Tilford, 1982).

Third, interpreting research on age and rank is also made difficult by large demographic variation among study samples. Demography varies naturally among study sites, among social groups within the same population, or in the same social group across time. Study sites often use different definitions of age classes, or researchers choose animals to fit their research topics. Interpreting data is made easier when researchers report age and rank for each individual in the sample, but not all studies do so (e.g. McMillan, 1989; van Noordwijk and van Schaik, 1988), or do not report additional data on tenure and natal status, even when known (e.g. Sprague, 1992). However, opportunities arise to examine these issues with studies that report data on each individual in a sample.

This paper reviews and reanalyzes data on age and rank among male macaques living in multi-male troops. The objective is to assess the role of demography on the age-rank correlation by focusing on whether: 1) non-linear regression finds significant curvature in age-rank relations, 2) age composition affects the significance of the regression, and 3) natal status and tenure are correlated with the residuals of the curvilinear regression.

METHODS

Seven studies were chosen that 1) provide data on at least age and rank for each individual in the sample, and 2) represent multi-troop populations where males can migrate freely (Table 1). The samples are named by study site and number for reference within the paper (e.g. Cayo Santiago 1). There are two samples of Japanese macaque (*M. fuscata*), four of rhesus macaque (*M. mulatta*), and one of barbary macaque (*M. sylvanus*). Five studies had reported a conclusion on the age-rank relation (Table 1). Similar studies were not reviewed here because they represented another example of the same site (Berard et al., 1993), or managed colony populations (Inoue, 1992; Smith, 1994).

TABLE 1. Sources and demographic compositions of data samples

Study site/dataset name	Yakushima	Arashiyama	La Parguera 1	La Parguera 2	Cayo Santiago 1	Cayo Santiago 2	Affenberg Salem
Species	fuscata	fuscata	mulatta	mulatta	mulatta	mulatta	sylvanus
Reference	Sprague, 1992	Norikoshi and Koyama, 1975	Drickamer and Vessey, 1973	Tilford, 1982	Hill, 1987	Chapais, 1983	Paul, 1989
Data year(s)	1984–1986	1972	1972	1979 (post-mating season)	1981	1978	1979
Population structure							
Troops in sample	10 troop-years	2 troops	4 troops	1 troop	1 troop	1 troop	1 troop
Troop ID's	A, M, H, P	A, B	A, C, I, E	A	I	F	B
Size/size range of troops	13–38	158 and 143	40–100	200	184	72	110
Provisioning	no	yes	yes	yes	yes	yes	yes
Population type	natural	free-ranging	island colony	island colony	island colony	island colony	enclosure
troops in population	multiple	2	4	10	multiple	multiple	multiple
Male membership							
Number/range in troops	3–8 males	26 and 26 males	7, 11, 14, 16 males	20 males	35 males	—	30 males
Sample size	59 male-years	52 males	48 males	20 males	15 males	14 males	30 males
Natal males in sample	—	8 males	2 males	14 males	1 male	2 males	8 males
Sample age composition							
Age range	small young—old	5–18+ years	3–15+ years	3–10 years	7–16 years	6–20 years	4–11 years
Years in age range	—	14+ years	13+ years	8 years	10 years	15 years	8 years
Age estimated for	—	6 males	9 males	none	none	none	5 males
Tenure counted from:							
for natal males	—	birth	birth	birth	birth	—	—
for non-natal males	—	troop fission	colony formation	birth	immigration	—	immigration
range	—	0.2–5.7 years	0.2–10+ years	2–6 years	5–9.5 months	—	>1 year
Original findings	Yes	Yes	Yes	—	No	—	Yes
age-rank correlation	—	Yes	Yes	—	Yes	—	—
rank-tenure correlation	—	—	—	—	—	—	—

—, not reported.

Demographic background

The study troops in the Yakushima site (Japanese macaque) had been habituated without any provisioning, and ranged freely within a large natural forest, surrounded by many other troops (Sprague, 1992; Takahata et al., 1994). The remaining studies represent provisioned, rapidly growing, and relatively large troops in populations with various numbers of troops. The Arashiyama population (Japanese macaque) consisted of two free-ranging troops in the year of the data used here (Norikoshi and Koyama, 1975; Huffman, 1991). The La Parguera and Cayo Santiago sites (rhesus macaque) are island colonies with multiple free-ranging troops (Drickamer and Vessey, 1973; Rawlins and Kessler, 1986). The Affenberg Salem site (barbary macaque) is a colony housing multiple free-ranging troops within an enclosure (Paul and Kuester, 1988).

Sample formulations varied among studies. The Yakushima sample pools data for the three to four troops that existed during a 3-year study period and the sample size is counted in male-years. The Arashiyama sample pools data from two troops in a single year. The La Parguera 1 sample pools data from four troops in a single year. The remaining four samples consist of single troops from single years.

Each sample has potential biases. Large, provisioned groups may represent the upper extremes in a species' range of group sizes. Pooling data across time or within one population creates the possibility of pseudo-replication. Single-troop samples may not be representative of a population or species because each troop is a temporally unique product of many demographic processes. The present analysis assumes that these issues do not seriously affect the results. Troop size per se is assumed to not alter a general tendency for age-graded rank relations, e.g. a 10-year-old male is assumed to have the same tendency to outrank a 4-year-old male regardless of troop size. In the only sample pooling data across both troops and time, the membership and ranks of males changed from year to year because of migration and troop fission. The single-troop samples show

moderate variation in age, natal status, and tenure.

Six studies provided numerical age; one study (Yakushima) provided age-class only. Age was known for studies on provisioned populations because most males had been born in the study populations, but even these estimated age or tenure for a few older or non-natal individuals. The analysis used N when age or tenure was estimated as $N+$ (i.e. 10+ years was treated as 10 years). Estimated ages are included in the analysis because removing them tends to truncate the upper age range. The Yakushima study provided only age-class because most males were non-natal immigrants that had joined the study troops from surrounding, unstudied troops; the youngest individual of known age was 4 years old.

Age composition varied considerably among study samples. Among studies reporting numerical age, lower age limits ranged from 3 to 7 years old, and the upper age limits from 10 to 20 years old. The age ranges covered varied from 8 to 15 years. The study providing only age class consisted of males from "small young" to "old" age classes.

Each study had determined dominance rank based on agonistic interactions. The reported ranks were used without modification. The ranges of dominance ranks vary among studies. While the highest dominance rank (no. 1) necessarily sets the upper limit, the lower limit is equivalent to the number of males in any single troop. The lowest (i.e. the numerically largest) rank in the analysis was 31st. In the figures showing rank on the y axis, the axis is reversed to display the no. 1 rank at the top.

Four studies reported tenure for each male in the sample (Arashiyama, La Parguera 1 and 2, Cayo Santiago 1). The reported tenures were used without modification. For non-natal males, all three studies measured tenure as time (years or months) since immigration. The lower limit of tenure depends on how researchers defined troop membership. The upper limit of tenure is usually the maximum number of years residence in a single troop, but two studies defined the upper limit of tenure differently: Arashiyama as years since a troop fission 6

years prior to the year of the data, La Parguera 1 as years since colony formation 10 years prior to the year of the data. For natal males, tenure is equivalent to age. However, for purposes of analysis, the 16-year-old natal alpha male in the Cayo Santiago 1 sample is assigned a tenure of 100 months.

Statistical analysis

For the studies providing numerical age, a second-order polynomial regression was applied to: 1) test for statistical significance in both the linear x and curvilinear x^2 components of the age-rank relation, and 2) use the residuals from the age-rank regression (called age-residual rank) in the analysis of tenure and natal status. The second-order polynomial regression is one of the simplest nonlinear regressions and assumes a hyperbolic curve. The ideal statistical method may be a non-linear, non-parametric regression similar to those being developed for morphological growth data (e.g. Moses et al., 1992), but developing such methods for social behavior is beyond the scope of this paper.

If the polynomial regression found a significant age-rank correlation, the younger age cohorts were successively removed from the sample until the regression lost statistical significance. R^2 is given whenever possible since the analysis depends on the loss of statistical significance after limiting or subdividing study samples. A reduced R^2 indicates that a loss of significance did not result solely from the reduced statistical power due to smaller sample size. A Kruskal-Wallis test was carried out on the study providing only age-class.

For the Arashiyama, La Parguera 1, and Affenberg Salem samples, an analysis of variance tested whether age-residual rank differed significantly between natal males and the other males in the troop. The relation between tenure and age-residual rank was investigated for the Arashiyama and La Parguera 1 samples. First, a linear regression was calculated between age-residual rank and tenure. Next, to account for potential heteroscedasticity in the age-tenure relation, males were divided into two subsamples: a new arrival group (tenure < 1

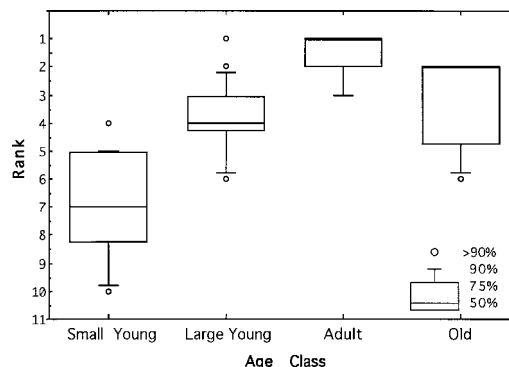


Fig. 1. Age and rank of male macaques: Yakushima, Japanese macaque. Data from Sprague, 1992. Rank-variation among age-groups: Kruskal-Wallis test, $N = 59$, $H = 39.5$, $P = 0.0001$.

year) and a long-staying group (tenure ≥ 1 year, and excluding natal males). The second-order polynomial regression with residuals, and the linear regression between age-residual rank and tenure, were recalculated for each subsample, with two exceptions. For the newly arrived male subsample of La Parguera 1, the age-residuals were calculated from a linear regression because the non-linear component was not significant. In the Arashiyama sample, there was too little variation in the newly arrived male subsample for further analysis.

RESULTS

The age classes occupied different ranks in the Yakushima sample (Fig. 1). The polynomial regression was statistically significant for the curved, as well as linear, portions of the age-rank relation in the Arashiyama, La Parguera 1, and Affenberg Salem samples (Figs. 2, 3, 4). The Affenberg Salem sample showed the highest R -squared ($R^2 = 0.89$). The males ranked almost perfectly according to age, with only two exceptions, one of which involved a natal male outranking an older male. No age-rank correlation was found for either the linear or curved portions of the polynomial regression in the Cayo Santiago 1, Cayo Santiago 2, and La Parguera 2 samples (Figs. 5, 6, 7).

The shape of the age-rank relation varied among samples. In the Yakushima sample, the "adult" age class held the highest ranks, the "small young" age class the lowest, and

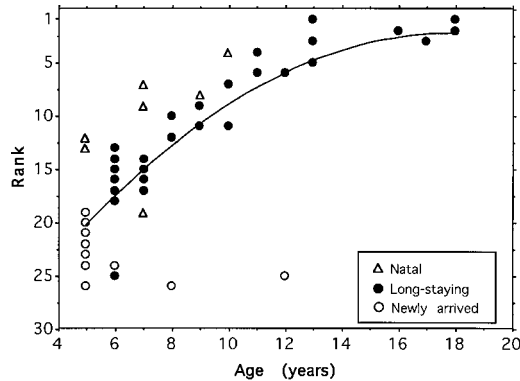


Fig. 2. Age and rank of male macaques: Arashiyama, Japanese macaque. Data from Norikoshi and Koyama, 1975. Second-order polynomial regression, $N = 52$, $R^2 = 0.63$, $F = 41.12$, $P = 0.0001$, x : $t = 3.88$, $P = 0.0003$; x^2 : $t = 2.32$, $P = 0.024$.

the "large young" and "old" age classes held intermediate rank. The regression drew an ascending slope for the Arashiyama, La Parguera 1, and Affenberg Salem samples. The regression curves peaked at about 10 to 18 years of age in these three samples, although it should be noted that the particular location of the peaks was an artifact of the regression. This was most obvious for La Parguera 1. The sample had no 10-year-old male at the peak of the age-rank curve, perhaps reflecting the 10-year-old history of the study site. The actual ages of top ranking males ranged from 6 to 20 years old.

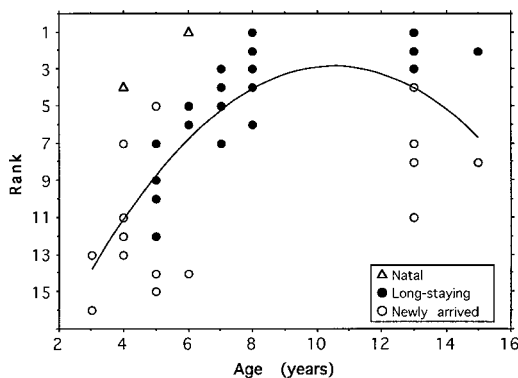


Fig. 3. Age and rank of male macaques: La Parguera 1, rhesus macaque. Data from Drickamer and Vessey, 1973. Second-order polynomial regression, $N = 48$, $R^2 = 0.46$, $F = 19.40$, $P = 0.0001$, x : $t = 4.61$, $P = 0.0001$; x^2 : $t = 3.98$, $P = 0.0002$.

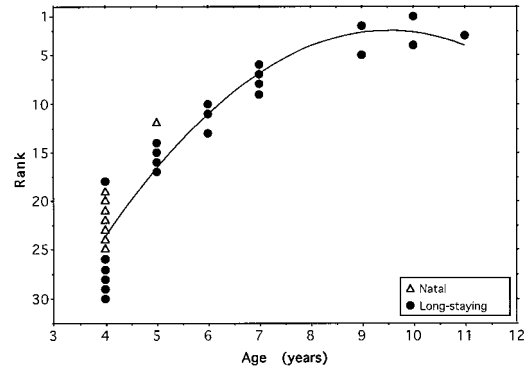


Fig. 4. Age and rank of male macaques: Affenberg Salem, barbary macaque. Data from Paul, 1989. Second-order polynomial regression, $N = 30$, $R^2 = 0.89$, $F = 113.64$, $P = 0.0001$, x : $t = 6.98$, $P = 0.0001$; x^2 : $t = 5.10$, $P = 0.0001$.

Rank appeared to decline with increasing age for some males in the Yakushima and La Parguera 1 samples, but not in other samples (Arashiyama, Affenberg Salem, Cayo Santiago 1, 2 and La Parguera 2). In the Yakushima sample, the "old" age class had lower rank than the adult age class (Fig. 1). The regression drew a descending slope for the La Parguera 1 sample (Fig. 3). Large variation among the 13- and 15-year-old males, including older, newly arrived males of low rank, accounted for the descending slope.

AGE COMPOSITION

The lower age limits of samples strongly affected the results of analysis. Excluding

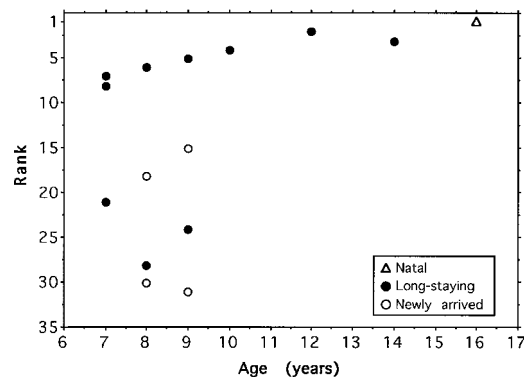


Fig. 5. Age and rank of male macaques: Cayo Santiago 1, rhesus macaque. Data from Hill, 1987. Second-order polynomial regression, $N = 15$, $R^2 = 0.26$, $F = 2.13$, $P = 0.16$.

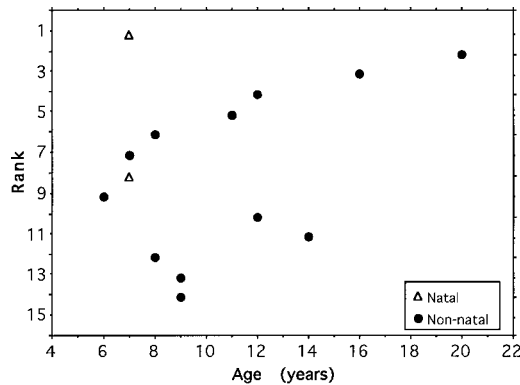


Fig. 6. Age and rank of male macaques: Cayo Santiago 2, rhesus macaque. Data from Chapais, 1983. Second-order polynomial regression, $N = 14$, $R^2 = 0.23$, $F = 1.60$, $p = 0.25$.

younger cohorts eliminated significant age-rank correlations, and at different lower age limits. Polynomial regressions lost statistical significance with age composition limited to males aged: ≥ 9 years for the Arashiyama sample ($N = 19$, $F = 2.25$, $R^2 = 0.22$, $P = 0.14$), ≥ 6 years for the La Parguera 1 sample ($N = 29$, $F = 0.93$, $R^2 = 0.066$, $P = 0.41$), and ≥ 9 years for the Affenberg Salem sample ($N = 5$, $F = 0.11$, $R^2 = 0.1$, $P = 0.9$).

Two studies not showing a significant age-rank relation had lower age limits of 7 years old (Cayo Santiago 1) and 6 years old (Cayo Santiago 2). The lower age limits had been set by the study goals of the researchers. The Cayo Santiago 1 sample was limited

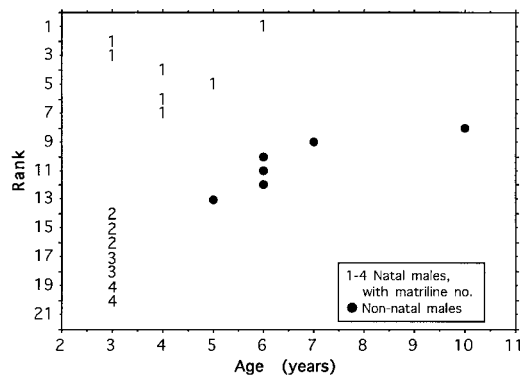


Fig. 7. Age and rank of male macaques: La Parguera 2, rhesus macaque. Data from Tilford, 1982. Second-order polynomial regression, $N = 20$, $R^2 = 0.17$, $F = 1.69$, $P = 0.21$.

to 15 adult males chosen out of the 31 males in the troop for a detailed behavioral study. The Cayo Santiago 2 sample focused on the 14 adult "central" males of the study troop.

Natal status and tenure

Even in samples showing strong age-rank correlations, large residual variation remained that can be partially explained by natal status and tenure. Natal males held significantly higher age-residual rank in the Arashiyama (ANOVA; $F = 10.63$, $P = 0.002$), La Parguera 1 (ANOVA; $F = 11.10$, $P = 0.0017$), and Affenberg Salem (ANOVA; $F = 6.05$, $P = 0.02$) samples. In addition, natal males held the top rank in the Cayo Santiago 1 and 2 samples, as well as in one troop in the La Parguera 1 sample.

In the La Parguera 2 sample, the many natal males may have overwhelmed the non-natal males to breakdown a potential age-rank correlation (Fig. 7). Natal males held both the highest and lowest ranks, with non-natal males in between. The top ranks were held by males of the same matriline and bottom ranks by males of other matriline. The non-natal males by themselves showed a significant age-rank correlation (linear regression, $N = 6$, $F = 10.84$, $R^2 = 0.73$, $P = 0.03$).

Tenure was significantly correlated with age-residual rank in the Arashiyama (linear regression, $N = 52$, $R^2 = 0.33$, $F = 24.75$, $P = 0.0001$) and La Parguera 1 (linear regression, $N = 48$, $R^2 = 0.24$, $F = 14.67$, $P = 0.0004$) samples, i.e. rank improved with increasing tenure regardless of age. In addition, tenure was correlated with rank alone in the Cayo Santiago 1 sample where no age-rank correlation existed (linear regression, $N = 15$, $R^2 = 0.61$, $F = 20.47$, $P = 0.0006$).

However, an age-independent tenure effect may not exist among males residing longer in a troop. Among the non-natal males of the La Parguera 2 sample, minimum tenure was 2 years, and tenure order was identical to age and rank order. For Arashiyama, with the sample limited to non-natal, long-staying males, there was no significant correlation between tenure and

age-residual rank (linear regression, $N = 30$, $F = 1.64$, $R^2 = 0.055$, $P = 0.21$). Nevertheless, the age-rank correlation remained significant among the long-staying males (polynomial regression, $N = 30$, $F = 91.34$, $R^2 = 0.87$, $P = 0.0001$; insufficient variation existed in the new-arrival subsample for further analysis). Similarly, for La Parguera 1, no significant correlation existed between tenure and age-residual rank with the sample limited to non-natal, long-staying males (linear regression, $N = 25$, $F = 0.22$, $R^2 = 0.0097$, $P = 0.64$). Furthermore, no significant relation existed between tenure and age-residual rank among the new arrivals by themselves (linear regression; $N = 21$, $F = 1.15$, $R^2 = 0.057$, $P = 0.29$). By contrast, the age-rank relation remained significant within both the long-staying and new-arrival subsamples (long-staying males: polynomial regression, $N = 25$, $F = 35.23$, $R^2 = 0.76$, $P = 0.0001$; newly arrived males: linear regression, $N = 21$, $F = 6.60$, $R^2 = 0.26$, $P = 0.019$).

DISCUSSION

The studies reviewed here exemplify the variability in the shape and internal dispersion of the age-rank relation in several populations of macaque males observed by different methods. No single statistical method could be applied to all the samples to explore whether an age-rank correlation existed. Nevertheless, the review showed that statistical analysis is likely to find a significant age-rank correlation in samples that encompass a broad age range, and include many non-natal males that had resided in a troop for at least 1 year. The age-rank relation is likely to have a significant degree of curvature. Thus, these samples may represent different parts of an inverted-U shaped age-rank relation of male macaques. There is less likelihood of finding a significant age-rank correlation in samples with a limited age range, or those that include many natal males or newly arrived males.

Age composition had a strong effect on whether statistical analysis found a significant age-rank correlation. The lower age limits varied between 6 to 9 years old among the samples in this review that showed no age-rank correlation. McMillan (1989), re-

porting no age-rank correlation among adults, had used a lower age limit of 6 years old. Researchers often deliberately define the lower age limit by the age at sexual maturity or "adulthood." Whatever the definition, adjusting the limit by just 1 or 2 years of age can radically alter the results of statistical analysis. Younger males are numerous, and may hold very different ranks compared to those just 1 or 2 years younger or older.

If reproductive success is correlated with age, then sample age composition may also affect whether statistical analysis finds correlations between rank and reproductive success. The Affenberg Salem sample (Paul, 1989) illustrates this point. Paul (1989) reported on the rank and mating success of males for 2 successive years on the same group. He found a significant correlation between rank and mating frequency for the adult age class in the second year, but not the first. The sample age composition differed between the 2 years. Paul (1989) defined "adult" to include males aged ≥ 7 years, and pointed out that the significant correlation depended partly on the low mating success of the 7-year-old cohort. However, the troop had no 7-year-old cohort in the first year producing the non-significant result. The 6-year-old cohort had grown up to join the adult age class in the second year.

The upper age range affects age-rank correlations if rank declines with age. Upper age ranges can vary easily among social groups depending on the survival or group membership of older individuals, although many studies define "adult" as all ages above a certain threshold. In the samples reviewed here, the upper age limits ranged from 10 years old to 20 years old. The former is quite young for animals that can live beyond 20 years of age (Huffman, 1991; Paul and Kuester, 1988). A descending age-rank slope balances the ascending age-rank slope, and has the effect of reducing the lower age limit of sample compositions that do not show significant age-rank correlations. The La Parguera 1 sample may be an example of this phenomenon, since it lost a significant correlation with the sample limited to males aged 6 years and above.

Whether rank declines for older males may depend on the demographic background of each sample, in particular, the prevalence of migration. Given the new-arrival effect on rank, immigrants account for many lower-ranking adult and older males. The La Parguera 1 sample had newly arrived males with ages of 13 and 15 years holding relatively low rank. By contrast, the Arashiyama and Cayo Santiago 1 samples had no older immigrants. Alternatively, in wild populations of some macaque species, prime adult males immediately acquire the most dominant rank upon joining a troop (Neville, 1968; Wheatley, 1982; van Noordwijk and van Schaik, 1985, 1988; Sprague, 1992; Takahata et al., 1994; Sprague et al., 1996). "Top-entry" has the effect of reducing the rank of prior residents and breaking down a rank-tenure relation. Former alpha males either remain in the troop at lower rank, or migrate to another troop where they may or may not be able to reacquire a high rank. The Yakushima sample includes three adult males that entered troops at the top rank. Two males aggressively took over the highest rank from the previous dominant male. The previous alpha males remained in the troop at lower rank. One adult male joined a fission troop as its first and dominant male. By contrast, in some populations, takeovers are extremely rare or absent (e.g. Arashiyama; Huffman, 1991; Sprague et al., 1996).

Top-entry may play larger roles in producing a descending slope in some species compared to those reviewed here. For example, several researchers have stated that baboon males often attain life-time peak dominance rank immediately upon entering a troop on their natal dispersal, while long tenure in a single troop is associated with gradually decreasing rank (Strum, 1982; Smuts, 1985; Altmann et al., 1988; Hamilton and Bulger, 1990).

Natal males tended to rank above non-natal males of similar age (Arashiyama, La Parguera 1), or natal males of a high-ranking matriline occupied the top ranks (La Parguera 1 and 2, Cayo Santiago 2). In most natural populations, natal males probably have little effect on the overall age-rank relation since males usually leave their na-

tal group (Colvin, 1986; Drickamer and Vessey, 1973; Koford, 1966; Mehlmen, 1986; Paul and Kuester, 1985; Sugiyama, 1976). Natal males may have a strong effect on age-rank correlations within small samples, colonies, or provisioned populations with many natal males (e.g. La Parguera 2).

Tenure may have had two opposing statistical effects on the age-rank relation in the Arashiyama and La Parguera 1 samples. On the one hand, a new-arrival effect weakened the age-rank correlation because many newly arrived males acquired low initial rank. On the other hand, long tenure in a single troop may have helped to reinforce an age-rank correlation.

One reason for this apparent contradiction may be that the age-tenure relation is heteroscedastic. The upper limit of the age-tenure relation is a line defined by $\text{tenure} = \text{age}$, corresponding to natal males remaining in the troop. For non-natal males, $\text{tenure} = \text{age} - [\text{age at troop entry}]$, and the lower limit of the age-tenure relation is a horizontal line close to zero. Thus, tenure is uncorrelated with age primarily during the earliest periods of male residence in a troop, and to the extent that males, especially adult or older males, acquire low age-specific rank at troop entry. When males live in the same troop for many years, tenure gradually comprises a higher proportion of age, and, in turn, loses an independent statistical effect on rank, while rank often rises gradually with the death or departure of higher ranking prior residents. New-arrival may also lose some effect if an age-rank correlation exists among the newly arrived males (e.g. La Parguera 1; Sprague, 1992). In some populations, the rank orders for dominance, tenure, and age may be similar or identical among non-natal males (La Parguera 2). This does not mean that all measures of tenure are irrelevant for long-time residents. Rather, the time length of tenure should be distinguished from order of arrival, which may influence dyadic rank relations for many years among males with very close age, rank, and tenure.

Many other demographic processes not covered in this review may affect the age-rank relation among macaque males. Age biases in male troop participation affects the

age composition of males residing in troops. Young males of many species form all-male groups, or dominant males exclude younger males from social groups (e.g. Newton, 1988). The survival curve affects cohort size and the proportion of older males present in the population. The larger, fast-growing, provisioned troops often have many same-aged individuals occupying different ranks, especially among younger age groups (Figs. 2–6). Variation in troop size creates variation in rank, since the number of ranks depends on troop size. The age-rank relation may be tightest for males living in a natural population, dispersed among many small troops of similar size, in which they are less likely to be living in the same troop with same-aged males.

The statistical analysis of dominance rank confined to a relatively narrow age range, in effect, targets the within-age effects of rank, while excluding cross-age effects. A sample confined to prime adult males focuses on variation near the peak of the age-rank curve, to the exclusion of younger or older males. This focus may be necessary for a study on the peak reproductive years of male primates. Nevertheless, research on the complete life-history of dominance rank effects may need to develop statistical techniques covering all age groups. A general approach may be to apply non-linear line-fitting techniques to fit age to reproductive success, and then investigate how rank and other variables account for both cross-age and within-age variation in reproductive success. The existence of a three-way association between age, rank, and reproductive success implies that rank may play a role in producing cross-age variation in reproductive success. Rank may reinforce a life history strategy delimiting reproduction to certain age groups. At the same time, rank may produce within-age variation in reproductive success, analogous to how tenure and natal status produce within-age variation in the age-rank relation.

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LITERATURE CITED

- Altmann J, Hausfater G and Altmann SA (1988) Determinants of reproductive success in savanna baboons, *Papio cynocephalus*. In TH Clutton-Brock (eds): Reproductive Success. Chicago: University of Chicago Press, pp. 403–418.
- Berard JD, Nürnberg P, Epplen JT and Schmidtke J (1993) Male rank, reproductive behavior, and reproductive success in free-ranging rhesus macaques. *Primates* 34:481–489.
- Bercovitch FB (1986) Male rank and reproductive activity in savanna baboons. *Int. J. Primatol.* 7:533–550.
- Bulger JB (1994) Dominance rank and access to estrous females in male savanna baboons. *Behaviour* 127: 67–103.
- Chapais B (1983) Matriline membership and male rhesus reaching high ranks in their natal troops. In RA Hinde (ed): *Primate Social Relationships*. London: Blackwell, pp. 171–175.
- Colvin JD (1986) Proximate causes of male emigration at puberty in rhesus monkeys. In RG Rawlins and MJ Kessler (eds): *The Cayo Santiago Macaques*. Albany: SUNY Press, pp. 131–157.
- Cowlshaw G and Dunbar RIM (1991) Dominance rank and mating success in male primates. *Anim. Behav.* 41:1045–1056.
- Dewsbury DA (1982) Dominance rank, copulatory behavior, and differential reproduction. *Q. Rev. Biol.* 57: 135–159.
- Drickamer LC and Vessey SH (1973) Group changing in free-ranging male rhesus monkeys. *Primates* 14: 359–368.
- Dunbar RIM (1988) *Primate Social Systems*. London: Croom Helm.
- Hamilton WJ and Bulger JB (1990) Natal male baboon rank rises and successful challenges to resident alpha males. *Behav. Ecol. Sociobiol.* 26:357–362.
- Hill DA (1987) Social relationships between adult male and female rhesus macaques: 1. sexual consortships. *Primates* 28:439–456.
- Huffman M (1991) History of the Arashiyama Japanese macaques in Kyoto, Japan. In L Fedigan and P Asquith (eds): *The Monkeys of Arashiyama: Thirty-five Years of Research in Japan and the West*. Albany: SUNY Press, pp. 21–53.
- Inoue M, Mitsunaga F, Ohsawa H, Takenaka A, Sugiyama Y, Soumah AP and Takenaka O (1992) Paternity testing in captive Japanese macaques (*Macaca fuscata*) using DNA fingerprinting. In RD Martin, AF Dixon, and EJ Wickings (eds). *Paternity in Primates: Genetic Tests and Theories*. Basel: Karger, pp. 131–140.
- Koford CB (1963) Rank of mothers and sons in bands of rhesus monkeys. *Science* 357:356–357.
- Koford CB (1966) Population changes in rhesus monkeys: Cayo Santiago, 1960–1964. *Tulane Studies in Zoology* 13:1–7.

- McMillan CA (1989) Male age, dominance, and mating success among rhesus macaques. *Am. J. Phys. Anthropol.* 80:83–89.
- Mehlmen P (1986) Male intergroup mobility in a wild population of the Barbary macaque (*Macaca sylvanus*), Ghomaran Rif Mountains, Morocco. *Am. J. Primatol.* 10:67–81.
- Moses LE, Gale LC and Altmann J (1992) Methods for analysis of unbalanced, longitudinal growth data. *Am. J. Primatol.* 28:49–59.
- Neville MD (1968) Male leadership change in a free-ranging troop of Indian rhesus monkeys (*Macaca mulatta*). *Primates* 9:13–27.
- Newton PN (1988) Variable social organization of hanuman langurs (*Presbytis entellus*), infanticide, and the monopolization of females. *Int. J. Primatol.* 8:59–77.
- Norikoshi K and Koyama N (1975) Group shifting and social organization among Japanese monkeys. In S Kondo, M Kawai, A Ehara, and S Kawamura (eds): *Proceedings Symposia 5th Congress International Primatological Society*. Tokyo: Japan Science Press, pp. 43–61.
- Paul A (1989) Determinants of male mating success in a large group of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *Primates* 30:461–476.
- Paul A and Kuester J (1985) Intergroup transfer and incest avoidance in semifree-ranging Barbary macaques (*Macaca sylvanus*) at Salem (FRG). *Am. J. Primatol.* 8:317–322.
- Paul A and Kuester J (1988) Life-history patterns of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. In JE Fa (ed): *Ecology and Behavior of Food-Enhanced Primate Groups*. New York: Alan R. Liss, pp. 199–228.
- Paul A and Kuester J (1996) Differential reproduction in male and female Barbary macaques. In JE Fa and DG Lindburg (eds): *Evolution and Ecology of Macaque Societies*. Cambridge: Cambridge University Press, pp. 293–317.
- Rawlins RG and Kessler MJ (1986) *The Cayo Santiago Macaques*. Albany: SUNY Press.
- Smith DG (1994) Male dominance and reproductive success in a captive group of rhesus macaques (*Macaca mulatta*). *Behaviour* 129:225–242.
- Sprague D (1992) Life history and male intertroop mobility among Japanese macaques (*Macaca fasciata*). *Int. J. Primatol.* 13:437–454.
- Sprague D, Suzuki S and Tsukahara T (1996) Variation in the social mechanisms by which males attained the alpha rank among Japanese macaques. In JE Fa and DG Lindburg (eds): *Evolution and Ecology of Macaque Societies*. Cambridge: Cambridge University Press, pp. 444–458.
- Smuts B (1985) Sex and Friendship In Baboons. New York: Aldine.
- Strum S (1982) Agonistic dominance in male baboons: An alternative view. *Int. J. Primatol.* 3:175–202.
- Sugiyama T (1976) Life history of male Japanese monkeys. In JS Rosenblatt (ed): *Advances in the Study of Behavior*, vol. 7. New York: Academic Press, pp. 255–284.
- Takahata Y (1982) Socio-sexual behavior of Japanese monkeys. *Z. Tierpsychol.* 59:89–108.
- Takahata Y, Sprague D, Suzuki S and Okayasu N (1994) Female competition, co-existence and the mating structure of wild Japanese macaques on Yakushima Island, Japan. In P Jarman and A Rossiter (eds): *Animal Societies: Individuals, Interactions and Organization*. Kyoto: Kyoto University Press, pp. 163–179.
- Tilford BL (1982) Seasonal rank changes for adolescent and sub-adult natal males in a free-ranging group of rhesus monkeys. *Int. J. Primatol.* 3:484–490.
- van Noordwijk MA and van Schaik CP (1985) Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). *Anim. Behav.* 33: 849–861.
- van Noordwijk MA and van Schaik CP (1988) Male careers in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour* 107:25–43.
- Wheatley BP (1982) Adult male replacement in *Macaca fascicularis* of east Kalimantan, Indonesia. *Int. J. Primatol.* 3:203–219.